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**Spatial patterns of African ungulate aggregation reveal complex but limited risk effects
from reintroduced carnivores**

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Abstract. The ‘landscape of fear’ model, recently advanced in research on the non-lethal effects of carnivores on ungulates, predicts that prey will exhibit detectable antipredator behavior not only during risky times (i.e., predators in close proximity) but also in risky places (i.e., habitat where predators kill prey or tend to occur). Aggregation is an important antipredator response in numerous ungulate species, making it a useful metric to evaluate the strength and scope of the landscape of fear in a multi-carnivore, multi-ungulate system. We conducted ungulate surveys over a two-year period in South Africa to test the influence of three broad-scale sources of variation in the landscape on spatial patterns in aggregation: 1) habitat structure, 2) where carnivores tended to occur (i.e., population-level utilization distributions) and 3) where carnivores tended to kill ungulate prey (i.e., probabilistic kill site maps). We analyzed spatial variation in aggregation for six ungulate species exposed to predation from recently reintroduced lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*). Although we did detect larger aggregations of ungulates in ‘risky places’, these effects existed primarily for smaller-bodied (<150kg) ungulates and were relatively moderate (change of ≤ 4 individuals across all habitats). In comparison, ungulate aggregations tended to increase at a slightly lower rate in habitat that was more open. Lion, an ambush (stalking) carnivore, had stronger influence on ungulate aggregation than hyena, an active (coursing) carnivore. In addition, places where lions tended to kill prey more strongly affected ungulate aggregation than places where lions tended to occur, but an opposing pattern existed for hyena. Our study reveals heterogeneity in the landscape of fear and suggests broad-scale risk effects following carnivore reintroduction only moderately influence ungulate aggregation size and vary considerably by predator hunting mode, type of predation risk, and prey species.

Key words: antipredator behavior; carnivore predation risk; landscape of fear; predator-prey interaction; risk effects; ungulate aggregation

INTRODUCTION

Examinations of predator-prey ecology have focused on direct, lethal predation effects on prey (Lima 1998), but recent work has expanded this view by quantifying non-lethal “risk effects” (i.e., altered prey behavior due to risk; Creel and Christianson 2008). These risk effects, which have been well-described in aquatic systems (e.g., Peacor and Werner 2001), are now being assessed in vast carnivore-ungulate systems. From this research, we understand that ungulates employ a variety of strategies to manage their interactions with carnivores. These include migrating to areas with lower carnivore densities (Hebblewhite and Merrill 2007), selecting habitat that provides cover (Valeix et al. 2009a, Thaker et al. 2011), and aggregating into larger groups as a means of additional vigilance, dilution, and defense (Hamilton 1971, Dehn 1990, Hebblewhite and Pletscher 2002). Predation-sensitive migration and habitat selection has been relatively well-documented in a variety of carnivore-ungulate systems (e.g., Hebblewhite and Merrill 2007, Valeix et al. 2009a), although understanding the demographic consequences of these behaviors remains a challenge. Comparatively, the factors shaping ungulate aggregation are more poorly understood, largely due to the complexity of herding behavior in heterogeneous environments (Pays et al. 2007, Fortin et al. 2009). For instance, whereas larger aggregations of ungulates can reduce predation risk via dilution, they can also result in decreased foraging efficiency (Molvar and Bowyer 1994). In addition, larger aggregations offer improved predator detection, but they are also more easily detected by predators (Caro 2005). Given that aggregation is one of the most common antipredator strategies employed by ungulates (Caro 2005), a more thorough understanding of the degree to which

spatial variation in risk from multiple carnivores influences ungulate aggregation is crucial to both predator-prey and behavioral ecology.

Several ungulate species in African systems modulate their group size in response to carnivore predation risk (Valeix et al. 2009b, Thaker et al. 2010, Creel et al. 2014). Whereas evidence suggests that ungulates aggregate when faced with predation risk in temporal dimensions (e.g., Valeix et al. 2009b), it is unclear how spatial aggregation patterns relate to predation risk. The “landscape of fear” model of predator-prey interactions (Laundré et al. 2001) predicts that antipredator processes such as aggregation will be detectable not only during risky times (i.e., when carnivores are in the immediate vicinity) but also in risky places (i.e., where carnivores typically occur or kill prey; Valeix et al. 2009a, Valeix et al. 2009b, Thaker et al. 2011, Creel et al. 2014). Although the landscape of fear theory has been presented as a framework for understanding broad-scale ecosystem dynamics (Ripple and Beschta 2004), the strength and scope of carnivore-induced risk effects are highly variable. For example, in African ecosystems, prey body size (Hopcraft et al. 2010), climate (Riginos 2015), and forage quality (Anderson et al. 2010) have been found to influence ungulate behavior as much or more than predation risk, while other work suggests interactive and context-specific effects of these factors (Sinclair and Arcese 1995). Furthermore, risk effects depend on predator hunting mode, with ambush predators generally eliciting the strongest prey responses (e.g., Schmitz 2008, Thaker et al. 2010).

Here, we aim to clarify the relative contribution of multiple forms of landscape-level predation risk on patterns of aggregation for six species of African ungulates exposed to multi-carnivore predation. A key objective of our study is to contextualize the top-down influence of carnivores on ungulate aggregation by comparing its effect size with that of an established

relationship between ungulate aggregation size and habitat structure (i.e., aggregations tend to be larger in more open habitat; Evans 1979, Gerard and Loisel 1995, Pays et al. 2007, Thaker et al. 2010, Marino and Baldi 2014). In addition, our study evaluates the hypothesis that carnivore risk effects on ungulates will vary by hunting mode and by prey species, as has been indicated in predator-prey systems across a diversity of taxa (Preisser et al. 2007).

To these ends, we conducted surveys over a two-year period in South Africa to quantify average ungulate aggregation size. We then compared spatial variation in ungulate aggregation to two types of risk associated with the primary carnivores in this system: 1) the probability of carnivore occurrence (population-level utilization distributions (UDs)) and 2) the probability of carnivore kill occurrence (probabilistic kill site maps). Given that both aggregation size and predation risk vary by ungulate species (Thaker et al. 2011, Gervasi et al. 2013), we developed this assessment at the level of each ungulate species.

METHODS

Study Area

We assessed spatial patterns in ungulate aggregation in the 132 km² fenced Main Camp section of Addo Elephant National Park, South Africa (Addo; 33°30'S, 25°45'E; Appendix A). The dominant habitat type in Addo is thicket with grassland sections in the east that are derivative of an agricultural history (Tambling et al. 2012). Unlike typical African savanna ecosystems, Addo lacks pronounced wet and dry seasons (e.g., average wet and dry season rainfall only differs by ~20mm; South African Weather Service, unpublished data). Using digital vegetation maps provided by South African National Parks, we identified six habitat types within Addo, including bushclump, gully thicket, thicket, Zuurkop woodland, long grassland, and short grassland (South African National Parks, unpublished data). The two primary

carnivores in the study area, lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*), were reintroduced in the Main Camp following a 100-year absence (Hayward and Hayward 2006). All lions (4M, 2F) and four hyenas (3M, 1F) were unrelated and were reintroduced in late 2003; an additional four unrelated hyenas (2M, 2F) were reintroduced in the winter of 2004 following a period of disease testing (see Hayward et al. 2007a, 2009). One leopard (*Panthera pardus*) also occurred in the study area but was not included in the analysis due negligible predation on the ungulate species of interest.

Ungulate surveys

Between December 2003 and November 2005, we conducted surveys to describe spatial variation in aggregation size for Cape buffalo (*Syncerus caffer*; hereafter buffalo), eland (*Tragelaphus oryx*), greater kudu (*Tragelaphus strepsiceros*; hereafter kudu), red hartebeest (*Alcelaphus buselaphus caama*), warthog (*Phacochoerus africanus*) and zebra (*Equus quagga*). These species occurred across the entire study area and were common prey of lion and hyena in Addo (Hayward 2006, Hayward et al. 2007b). We conducted vehicle-based surveys on a network of 51 transects (\bar{x} transect length = 913 m, range 567 – 1,029 m; Appendix A). We conducted surveys three hours preceding and following dawn and dusk, using spotlights when necessary. These time periods correspond with peak activity times for lions and hyenas in Addo (Hayward and Hayward 2006). We conducted 30 surveys per year on randomly selected days and varied the start location for surveys to eliminate temporal bias at any given location. We recorded aggregation size at the start, middle, and end points of each transect. The same observer conducted each survey alongside a scribe. Detections occurred without the aid of binoculars, although counts were confirmed using binoculars. In most cases (i.e., >80%), only one aggregation of a given species was present at a transect point during a given survey. When

multiple, distinct groups of the same species were seen at a given location, we first corrected group size via distance sampling to accommodate variation in visibility by regressing the log of group size against the estimated detection probability in each habitat type (Buckland et al. 2001). We then summed group sizes to obtain species-specific aggregation sizes. We considered groups distinct when individuals were closer to other members of their group than the nearest peripheral members of another group. We counted all individuals (i.e., adults and juveniles) and assumed counts close to the line were accurately recorded (Buckland et al. 2005). Thus, aggregations represent all individuals of the same species at a transect point at a given time, whether one distinct aggregation or an aggregation of two or more groups in close proximity to the transect point.

Carnivore occurrence models

We developed population-level UD for lions and hyenas to model predation risk as a function of carnivore occurrence (Hebblewhite and Merrill 2007, Valeix et al. 2009, Thaker et al. 2011). We VHF-tracked the entire lion population ($N = 6$) and 75% ($N = 6$) of the adult hyena population for two years following release in Addo. Both lions and hyenas were consistently tracked throughout the two-year study period via continuous, 96-hour follows conducted on average once every six weeks; opportunistic observations of carnivore locations and kills were also recorded outside these times (see Hayward et al. 2009). As with ungulate surveys, carnivore location data were primarily collected during times when lions and hyenas were most active (i.e., within 3 three hours of dawn and dusk; Hayward and Hayward 2006, Hayward et al. 2009). In this way, we attained an average of 48 locations ($SD = 18$) per hyena ($N = 285$ total locations for 6 hyenas) and 103 locations ($SD = 23$) per lion ($N = 615$ total locations for 6 lions). Beginning in November 2003, we partitioned lion locations into three, four-month periods per year through

October 2005: summer (November – February), autumn/early winter (March – June), and late winter/spring (July – October). We then mapped population-level lion UD for each period to account for temporal variation in lion ranging patterns following reintroduction (i.e., range expansion; Hayward et al. 2009). Given the lower sample size of hyena locations ($N = 285$), we developed a pooled UD representing population-level hyena space use over the two-year period (Seaman et al. 1999). We developed UDs in R (R Development Core Team 2011) using a bivariate plug-in matrix (Gitzen et al. 2006). We depicted the interpolated density estimates as UD percentiles at a 30m^2 resolution such that the highest percentile (100) represented the very core of the UD, while the lowest percentile (1) represented the periphery. Areas not encapsulated by any portion of the UDs had a value of 0, representing a negligible probability of carnivore occurrence.

Kill occurrence models

We identified carnivore-killed ungulates via continuous follows and incidental sightings. We distinguished lion kills from those of hyenas based on observations of hunts and kills, signs and direct observations of feeding on fresh carcasses. We saw no indication of intraguild scavenging between lions and hyenas during continuous follows and have no other evidence of its occurrence, as both species were at low densities during our study period.

We used the locations of killed ungulates to develop probabilistic spatial models of kill occurrence throughout the study area as a function of landscape characteristics, which were assigned using a lattice comprised of 250m^2 cells in ArcMap Version 10. We identified relevant landscape covariates *a priori* for both lion and hyena kill occurrence models. These included the proportion of each habitat type and the length of hard edge within a cell, in addition to the Euclidean distance from kill site to fenceline, waterholes ($N = 11$), and campsites ($N = 2$). Given

that lions use cover to ambush prey (Loarie et al. 2013) and frequently kill near edge habitat (Prins and Iason 1989), we defined hard edge as the boundary between open (short and long grassland) and closed habitats (gully thicket, thicket, Zuurkop woodland, and bushclump). We included the fenceline, waterhole, and campsite covariates to account for increased carnivore hunting success near fences (Davies-Mostert et al. 2013), variation in ungulate water dependency (Valeix et al. 2009b) and carnivore/ungulate avoidance of anthropogenic infrastructure (Howe et al. 2013). For lions, we evaluated both a pooled model (using all locations of lion-killed ungulates) and species-specific models (e.g., using only locations of lion-killed buffalo to develop a lion-buffalo kill occurrence map) for ungulate species with sufficient sample size of kill sites ($N \geq 25$; buffalo, kudu, and warthog). However, preliminary model analyses using Akaike's Information Criterion corrected for sample size (AIC_c) indicated that, for each ungulate species, the pooled model of lion-killed ungulates was better supported by the data than species-specific models. Therefore, we used the pooled model in subsequent analyses for all six ungulate species. For hyena, we did not have sufficient sample sizes to evaluate species-specific models, thus we built the hyena kill occurrence model using pooled locations of all hyena-killed ungulates. The smaller sample size of hyena-killed ungulates was unsurprising given that hyenas exhibit non-specific predation tendencies and lower preference for our focal ungulate species than lions (Hayward 2006).

Using a case-control design, we compared the landscape covariates of the locations of each recorded lion ($N = 172$) or hyena ($N = 50$) kill site to landscape covariates associated with 20 random locations in k strata, where each stratum is a matched set consisting of the kill location and 20 random locations (Hosmer and Lemeshow 2000, Manly et al. 2002). We enforced a minimum distance of 500m such that none of the random controls were associated

with the exact habitat conditions of the kill sites (Gervasi et al. 2013). We used a mixed effects logistic regression procedure and modeled the k_{ith} stratum as a random effect. We evaluated all linear, non-interacting combinations of the *a priori* covariates described above and ranked models according to AIC_c weight (w_i ; Burnham and Anderson 2002). Given that our primary goal was prediction, we averaged parameter estimates over all models with a cumulative AIC_c w_i of 0.95 (Burnham and Anderson 2002:150). We used the resultant averaged parameter estimates to produce an odds ratio of kill occurrence (Keating and Cherry 2004) that took form:

$$\Psi(\chi|\chi_R) = \exp [\beta_1(\chi_1 - \chi_R) + \beta_2(\chi_2 - \chi_R) + \dots + \beta_n(\chi_n - \chi_R)] \quad (1)$$

where $\Psi_{(\chi)}$ is the relative probability of kill occurrence in a given 250 m cell, χ_n is the covariate value of that cell, and χ_R is the mean covariate value of all cells in the study area. Given that predation events are rare throughout the study area, we can interpret the odds ratio as an approximation of the relative probability of kill occurrence (Keating and Cherry 2004), where $\Psi(\chi|\chi_R) = 1.0$ represents the mean probability of kill occurrence. Values lower or higher than 1.0 represent changes in the odds ratio of kill occurrence (e.g., $\Psi(\chi|\chi_R) = 2.0$ indicates a location with twice the relative probability of kill occurrence than the mean; Fig. 1).

To assess the predictive ability of the kill occurrence models, we conducted k-folds cross validation tests (Boyce et al. 2002). We divided the data between training and testing portions maintaining an 80:20 ratio and fit kill occurrence models using the training data and validated the predictions with the testing data. We conducted this test five times and partitioned the predictive output into 10 categories. We compared the training and testing data using Spearman-rank correlation coefficients (r_s ; Boyce et al. 2002).

Ungulate aggregation models

We used the average ungulate aggregation size for each species at each transect point and within each period as the response variable in our ungulate aggregation models. We fit spatially-explicit mixed effects linear regression models to predict spatial variation in average ungulate aggregation in relation to carnivore occurrence and kill occurrence. These models took the form:

$$Y_{ij} = X\beta_{ij} + Zu_j + e \quad (2)$$

where Y_{ij} is the log-transformed average ungulate aggregation size at the i th transect point in period j , $X\beta_{ij}$ is a vector of the predictor covariates at the i th transect point in time period j (only lion UD were separated by period), and Zu_j is the random effect term for each time period in the assessment (3 periods in each year such that $N_j = 6$). For all models, we accounted for spatial autocorrelation among the i th transect points by using an exponential covariance structure, as determined by AIC_c (Zuur et al. 2009). Prior to model fitting, we examined multicollinearity to avoid excessive covariate correlation (0.7 tolerance level).

We took a two-step information theoretic approach to model selection to balance precision and bias in our final models (Burnham and Anderson 2002). In the first step of model selection, we built a global model *a priori* that included carnivore UD, carnivore kill occurrence, amount of hard edge (linear length in meters), and degree of openness (proportion of open habitat within a 250m² cell). We included hard edge and openness covariates due to associations between open habitats, increased visibility, and aggregations of African ungulates (Evans 1979, Gerard and Loisel 1995, Pays et al. 2007, Creel et al. 2014, Marino and Baldi 2014). We then evaluated models developed from all possible linear combinations of these six covariates. Interaction terms were not considered due to lack of clear justification and a desire to keep the candidate model set as small as possible (Burnham and Anderson 2002:17). We ranked models based on AIC_c and assessed models based on $AIC_c w_i$ (Burnham and Anderson 2002).

Aggregations of a given species might be influenced by the presence of other ungulates (Scheel 1993). Accordingly, the second step of our model selection process tested whether the top model for each ungulate species could be improved by the sequential addition of covariates representing aggregations of other ungulate species at the i th transect point in the j th period. These covariates were not considered in the first step of the model selection process because we could not hypothesize ungulate species associations in an *a priori* fashion and because an all combinations approach would have undermined model parsimony by resulting >2000 candidate models (Burnham and Anderson 2002:174). Thus, we assessed whether the fit of the top-ranking model from the first model selection step could be improved by the iterative addition of covariates representing the other ungulate species, as assessed by a significant likelihood ratio test ($\alpha = 0.05$ cutoff; Zuur et al. 2009). We concluded this process when the addition of parameters no longer improved model fit and ranked final models using AIC_c and $AIC_c w_i$. We averaged parameter coefficients across all models within $1/8^{th}$ $AIC_c w_i$ of the top-ranking model (Burnham and Anderson 2002:171). We calculated the relative importance of covariates X_j by summing Akaike weights across models where covariate j occurred (Burnham and Anderson 2002:168). Finally, we plotted model-averaged coefficients for all parameters with a significance of $\alpha \leq 0.01$ to examine covariate effect size.

RESULTS

We recorded 4,964 observations of ungulates, 615 lion locations, and 285 hyena locations during the two-year survey period. Population-level lion UD varied by time period, with home range expansion occurring over the two-year reintroduction period (Appendix B). Population-level hyena UD were focused around denning sites in the southwestern portion of the Main Camp (Appendix B). Ungulate aggregation distributions were right-skewed; mean aggregation sizes for the six species ranged from 2.8 to 16.7, with warthog forming the smallest aggregations

and buffalo forming the largest (Appendix C). We located 172 lion-killed ungulates and 50 hyena-killed ungulates. For both lion and hyena, kudu was the most commonly killed ungulate (34.3% [N = 59] of all lion kills and 40.0% [N = 20] of all hyena kills) and zebra was the least common (1.7% [N = 3] of all lion kills and 2.0% [N = 1] of all hyena kills).

Both the lion and hyena kill occurrence models revealed substantial spatial variation in kill occurrence across the study area (Fig. 1). The k-folds cross validation tests indicated a good fit of the models to the data, with an average correlation among the training and testing data of $r_s = 0.921$ and $r_s = 0.916$ for the lion and hyena models, respectively. For the lion model, the relative probability of lion kill occurrence was positively associated with length of hard edge and proportion gully thicket and negatively associated with distance to campsites; the highest probability of lion kill occurrence was where gully thicket habitat formed a hard edge with open habitat (Appendix D, Fig. 1). For the hyena model, the relative probability of hyena kill occurrence was negatively associated with distance to waterhole and distance to fenceline and positively associated with length of hard edge (Appendix E). Hyena kill occurrence was greatest in open habitat (Fig. 1).

For each ungulate species, the addition of covariates representing aggregations of the other ungulate species failed to improve the top model and thus those covariates are absent in final model sets. Buffalo aggregation size was best described by a univariate model representing degree of openness and the open covariate was the most important covariate in the model set (Table 1, Fig. 2a). No covariate was significantly associated with buffalo aggregation size at the $\alpha < 0.05$ level (Appendix F). For eland, hyena occurrence featured as a covariate in each of the top four models (Table 1) and had the highest relative importance in the model set (Fig. 2b). For kudu and hartebeest, the top four models for both species featured the open, lion kill occurrence,

and hyena occurrence covariates and these three covariates had the highest relative importance over the model set (Table 1, Fig. 2c,d). In the case of kudu, lion kill occurrence and proportion open habitat were both highly significant predictors of aggregation size ($P < 0.0001$, Appendix F). For example, kudu aggregations increased from an average of ~ 2 individuals in completely closed habitat to ~ 4.5 individuals in completely open habitat (Fig. 3a). Similarly, as the odds ratio of lion kill occurrence increased twelve-fold from 0.5 to 6.0, the average aggregation size of kudu increased from ~ 2 individuals to ~ 5 (Fig. 3b). For red hartebeest, these two covariates (proportion open habitat and lion kill occurrence) were also highly significant ($P < 0.01$, Appendix F) and showed a similar positive association. For example, average hartebeest aggregations increased from an average of ~ 3 individuals in completely closed habitat to ~ 5 individuals in completely open habitat (Fig. 3c) and from ~ 3 individuals to ~ 7 as the odds ratio of lion kill occurrence increased from 0.5 to 6.0 (Fig. 3d). For warthog, the open and lion kill occurrence covariates featured in all of the top four models (Table 1) and both had a relative importance near 1.0 over the model set (Figure 2e). The positive association between warthog aggregation size and lion kill occurrence was highly significant ($P = 0.01$, Appendix F); as the odds ratio of kill occurrence increased from 0.5 to 6.0, warthog aggregations increased from an average of ~ 2 individuals to ~ 3 (Fig. 3e). Finally, for zebra the open and edge covariates featured in all of the top four models (Table 1) and these two metrics both had a relative importance near 1.0 over the model set (Fig. 2f). Of these, the open covariate had a highly significant ($P < 0.01$) positive association with zebra aggregation size; zebra aggregations increased from an average of ~ 3 individuals in completely closed habitat to ~ 4 in completely open habitat (Fig. 3f).

DISCUSSION

A recent wave of research has advanced our understanding of non-lethal effects of carnivores on ungulates, but generalizing these risk effects over broad terrestrial scales has proven difficult (e.g., see Kauffman et al. 2010). Over a two-year period, we found that ungulate aggregation size was positively associated with increased predation risk and habitat openness, but the effects of both of these factors were moderate and varied by carnivore hunting mode and prey species (Preisser et al. 2007). The final models predicting ungulate aggregation size were largely multivariate and often contained several important covariates (Fig.2), highlighting the idea that no single influence drives ungulate aggregation (Creel et al. 2014). Given that top predators were absent from Addo for 100 years preceding our study and that reintroduced carnivores existed in low densities, the risk effects we observed might be smaller in magnitude when compared to systems with non-naïve prey (Berger 2001) or high predator densities (Peacor and Werner 2001). Moreover, given the coarse-grain scale of our study (i.e., population-level spatial tendencies of carnivore occurrence and kill sites over two years), we view our conclusions as relevant to broad spatial scales of predation risk rather than finer-scaled responses (e.g., increased vigilance as a predator approaches; Périquet et al. 2010). Therefore, despite the established general principle that prey tend to aggregate in response to heightened predation risk (Caro 2005), application of this antipredator defense strategy is scale-specific and dependent upon habitat structure, the type and duration of predation risk, prey naiveté, and the ungulate species in question. We do not view our study as an explicit test of top-down versus bottom-up effects on ungulate aggregation. However, given the correlation between habitat structure and forage availability and quality, our study suggests that complex top-down effects act in tandem with bottom-up habitat features to shape prey response to predation risk (Jarman 1974, Anderson et al. 2010, Hopcraft et al. 2010).

Our results suggest that, like a complex physical landscape, the landscape of fear can be highly heterogeneous. We note two sources of variation in the landscape of fear in Addo: 1) carnivore identity, and 2) the nature of predation risk. In our study, spatial variation in lion kill occurrence was a more important factor for predicting ungulate aggregation size than lion occurrence, the latter having generally low importance (Fig. 2). Others have found the presence of lions influences ungulate behavior, either by increasing vigilance (Hunter and Skinner 1998, Périquet et al. 2010), altering habitat selection and space use (Valeix et al. 2009a, Thaker et al. 2010, 2011), or limiting access to quality forage (Barnier et al. 2014). Taken in context with our results, this suggests that ungulates employ multiple strategies to mitigate interactions with lions. For example, whereas ungulates might prefer more open habitats and increase vigilance in response to fine-scale risk (e.g. a lion in close proximity; Valeix et al. 2009b), they might aggregate in especially dangerous locations at broader scales (Thaker et al. 2010, this study). Moreover, in the face of consistent, long-term (i.e., >3 years) exposure to predation, some ungulates might form large herds (i.e. > 100 individuals; Tambling et al. 2012) or migrate to areas of lower risk (Hebblewhite and Merrill 2007).

In contrast with these lion-related effects, the influence of hyena on ungulate aggregation was weaker and more strongly linked to where hyenas tended to occur rather than where they tended to kill (Fig. 2). This difference appears to be driven in part by the opposing patterns of kill occurrence of lions and hyenas in our study (Fig. 1). Given that covariates for lion and hyena kill occurrence often occurred in top models together (Table 1) but did not always have opposing coefficients (Appendix F), the effect of the opposing patterns in kill occurrence on ungulate aggregation likely arose from differences in hunting behavior rather than as a mere artefact of negatively correlated spatial kill patterns between lions and hyenas. Thus, our results

corroborate the disparity of influence from active (coursing) versus ambush (stalking) predators that has been shown in smaller systems (e.g., Schmitz 2008). Creel et al. (2014) found that African ungulate group size was more influenced by hyena presence than lion presence and suggested ambush predators might have weaker effects in carnivore-ungulate systems than in invertebrate systems (e.g., Schmitz 2008). Our study sheds light on this discrepancy by decomposing risk from carnivores with differing hunting modes into two distinct expressions, namely, where they tend to occur and where they tend to kill. With this level of resolution, our results suggest that the active carnivore (hyena) tends to influence ungulate aggregation via occurrence while the ambush carnivore (lion) tends to influence via a tendency to kill in specific locations. However, as in Creel et al. (2014), the influence of these factors varied considerably among our focal ungulate species, highlighting the need for additional research to test this generalization in carnivore-ungulate systems

Habitat structure was also associated with ungulate aggregation for several species. Early research posited that ungulates aggregated in open habitat to decrease predation risk via dilution (Jarman 1974). However, more recent theoretical (Gerard and Loisel 1995) and experimental (Pays et al. 2007) studies have shown that open areas facilitate aggregation simply by virtue of improved visibility and conspecific detection. In our study, the degree of habitat openness consistently featured in the top models for most species (Table 1, Fig. 2). However, with respect to lion kill occurrence, open habitat was relatively safe (Fig. 1). Therefore, our work corroborates the notion that predation and openness can act independently to shape group size in ungulates (Marino and Baldi 2014), although these factors might be interactive for some species (Thaker et al. 2010). The edge formed between open and closed habitat is especially dangerous for African ungulates (Prins and Iason 1989). However, the amount of hard edge was generally a

less important aspect of habitat structure for ungulate aggregation compared to the level of openness (Fig. 2), emphasizing the importance of visibility over access to cover, as has been reported for other African ungulates (Riginos 2015).

Our models for buffalo suggest that neither predation risk nor habitat structure were strongly related to aggregation size (Table 1, Appendix F). This lack of effect corroborates the notions that buffalo “basically ignore lions” (Prins and Iason 1989:290) and that risk-induced behavioral modifications are weaker in large-bodied ungulates (Hopcraft et al. 2012). Rather than aggregating, buffalo might shift habitat selection to avoid risky areas (Valeix et al. 2009a, 2009b), a pattern that has also been recorded for giraffe (*Giraffa camelopardalis*; Creel et al. 2014). Recent work in Addo using long-term (i.e., 14 years) data found that, following lion reintroduction, small buffalo herds amalgamated into a large herd that provided protection for juvenile buffalo; however, this change required more than three years to take place (Tambling et al. 2012). Hence, behavioral adaptations in ungulates following reintroduction might need several years to actualize for naïve prey (Berger 2001). Understanding how risk effects vary over time, especially in relation to naïve ungulate prey facing reintroduced carnivores, is an important topic for future research.

Species-specific strategies for minimizing predation risk are poorly understood in multi-carnivore systems (Thaker et al. 2011, Creel et al. 2014). We noted distinct responses among six ungulate species. The two largest ungulates, buffalo and eland, showed the least response to risk and had the highest model uncertainty (Table 1, Fig. 2, Appendix F). These two species had the largest aggregations on average (Appendix C) and both can successfully defend against lion attacks (Caro 2005), thus their response to predation risk is perhaps more closely tied to a few very large herds capable of self-defense rather than smaller aggregations of individuals

throughout the study area (Tambling et al. 2012). Moreover, the lack of risk effects on buffalo, eland, and zebra (Fig. 2a,b,f) support the conclusion of Sinclair et al. (2003) that the influence of top-down predation rapidly declines as prey body size increases beyond 150kg (zebra, the smallest of these three species, has an average body size of 175kg; Stuart and Stuart 2000). The final models for red hartebeest, kudu and warthog (Table 1, Fig. 2c,d,e; Appendix F), further corroborate stronger influence of predation risk on small-bodied (<150kg) ungulates (Sinclair et al. 2003, Hopcraft et al. 2012). However, whereas the associations between lion predation and aggregation in these three smaller-bodied species were significant ($P \leq 0.01$, Appendix F), the magnitude was moderate (Fig. 3b,d,e). For example, the greatest degree of association between spatial aggregation and lion kill occurrence among these three species was in red hartebeest, with aggregations increasing from ~3 to ~7 individuals on average across the full range of risk (e.g., the odds ratio of lion kill occurrence in the most dangerous locations was >10 times that of the safest places, Fig. 1, Fig. 3d). Nominal effects of predation risk on ungulate group size have similarly been reported in both experimental (Hunter and Skinner 1998) and observational studies (Valeix et al. 2009b, for exception see Thaker et al. 2010). However, more pronounced risk effects might be expected in systems with non-naïve prey or higher predator densities (Peacor and Werner 2001). For instance, lion density in our study was 0.045 lions/km², which is lower than systems such as Kruger National Park (0.07 lions/km²) or the Serengeti (0.14 lions/km²; Hayward et al. 2007c). Similarly, prey response to risk might be more pronounced at finer spatial scales (e.g., when a predator is in the immediate vicinity of prey). Risk effects from wide-ranging carnivores vary over spatial scales (Hebblewhite and Merrill 2007), suggesting that, like many ecological processes, comparisons of risk effects are likely scale-dependent (Levin 1992). Accordingly, our inferences apply at a relatively coarse spatiotemporal scale (i.e.,

analogous to Johnson's (1980) second or third order) and do not necessarily preclude stronger risk effects at finer-scales.

Our findings highlight the complexity inherent in broad-scale, multi-carnivore, multi-ungulate systems and suggest that understanding the strength and scope of carnivore risk effects, along with associated implications for ungulate demography and ecosystem function, remains a substantial challenge. Moreover, evaluating the numeric prey response to reintroduced predators is also important, both for understanding patterns in ungulate aggregation (Hebblewhite and Pletscher 2002) and predicting the long-term impacts of top predators on trophic interactions (Peterson et al. 2014). Hence, we view our findings of moderate, coarse-grain risk effects on naïve prey over a two-year period as reason to echo the call of Tambling et al. (2012) for robust, long-term monitoring of African carnivore reintroductions in order to place non-lethal behavioral responses within the context of the numeric and functional responses in multi-predator, multi-prey systems. Studies that disentangle the effects of 'risky times' (carnivores in close proximity) and 'risky places' (locations of probable carnivore occurrence or kills) at multiple spatial scales (sensu Johnson 1980) would be particularly insightful. Lastly, we encourage researchers to build upon our study by incorporating explicit measures of forage into evaluations of carnivore risk effects on ungulates.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A-F are available online: URL

Appendix A. Study area and transect locations.

Appendix B. Utilization distributions (UDs) of lions and hyenas.

Appendix C. Ungulate aggregation sizes.

Appendix D. Lion (*Panthera leo*) kill occurrence model.

Appendix E. Spotted hyena (*Crocuta crocuta*) kill occurrence model.

Appendix F. Model-averaged coefficients for ungulate aggregation models.

Table 1. Models describing aggregation of ungulates exposed to multi-carnivore predation in the Main Camp section of Addo Elephant National Park, South Africa (2003-2005) after a two-step information theoretic model selection procedure. Top four models shown for clarity.

	Model covariates [†]	k	ΔAIC_c	w_i
Buffalo	Open	6	0	0.13
	HyenaKill	6	1.23	0.07
	Open + LionKill	7	1.43	0.06
	Null (Intercept only)	5	1.45	0.06
Eland	LionKill + HyenaUD	7	0	0.07
	LionUD + HyenaUD	7	0.35	0.06
	HyenaUD	6	0.42	0.05
	LionKill + LionUD + HyenaUD	8	0.48	0.05
Kudu	Open + Edge + LionKill + LionUD + HyenaKill + HyenaUD	11	0	0.21
	Open + LionKill + LionUD + HyenaKill + HyenaUD	10	0.37	0.17
	Open + Edge + LionKill + HyenaKill + HyenaUD	10	0.79	0.14
	Open + LionKill + LionUD + HyenaUD	9	1.78	0.09
Red	Open + Edge + LionKill + HyenaUD	9	0	0.36
hartebeest	Open + Edge + LionKill + HyenaKill + HyenaUD	10	1.28	0.19
	Open + LionKill + HyenaUD	8	1.7	0.15
	Open + Edge + LionKill + LionUD + HyenaUD	10	2.11	0.13
Warthog	Open + LionKill	7	0	0.28
	Open + LionKill + HyenaUD	8	1.84	0.11

	Open + Edge + LionKill	8	1.93	0.11
	Open + LionKill + LionUD	8	1.94	0.11
Zebra	Open + Edge	7	0	0.2
	Open + Edge + LionKill	8	0.76	0.14
	Open + Edge + LionUD	8	1.49	0.1
	Open + Edge + HyenaKill	8	1.57	0.09

627 *Notes:* k = number of model parameters; w_i = AIC_c weight for the i th model.

628 [†]Covariate definitions: Open = proportion open habitat, Edge = length of hard edge, LionKill =
 629 odds ratio of lion kill occurrence, LionUD = lion UD percentile, HyenaKill = odds ratio of hyena
 630 kill occurrence, HyenaUD = hyena UD percentile.

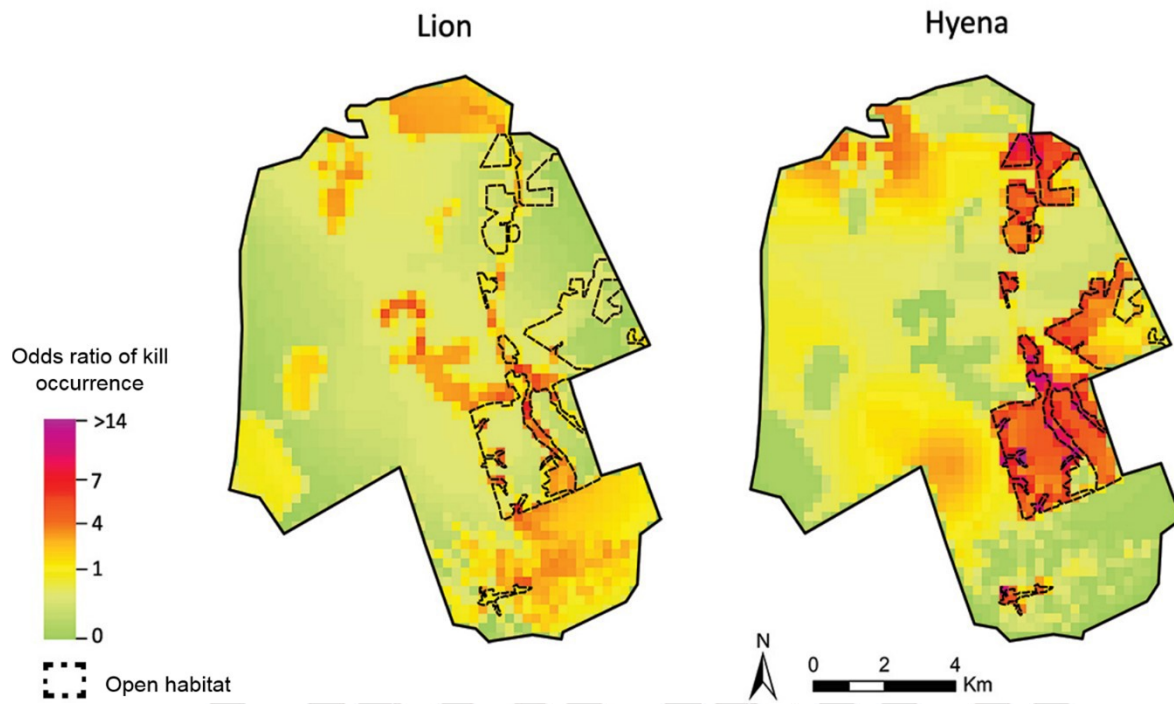
FIGURE LEGENDS

Figure 1. Odds ratios of lion and hyena kill occurrence of six ungulate species (buffalo, eland, kudu, red hartebeest, warthog, and zebra) at 250m² resolution in the Main Camp section of Addo Elephant National Park, South Africa (2003-2005). The odds ratio scale of predation applies to both maps, but given the higher prevalence of lion predation, risky areas in the lion map are riskier than similarly colored areas in the hyena map. Green and red/purple areas represent the lowest and highest odds ratios of kill occurrence, respectively. Open habitat is identified by the overlaid dashed polygons; all other habitat was classified as closed.

Figure 2. Relative importance of covariates in final model sets describing ungulate aggregation in Addo Elephant National Park, South Africa (2003-2005). The numbers above each bar are relative importance values of a given covariate rounded to two decimal places.

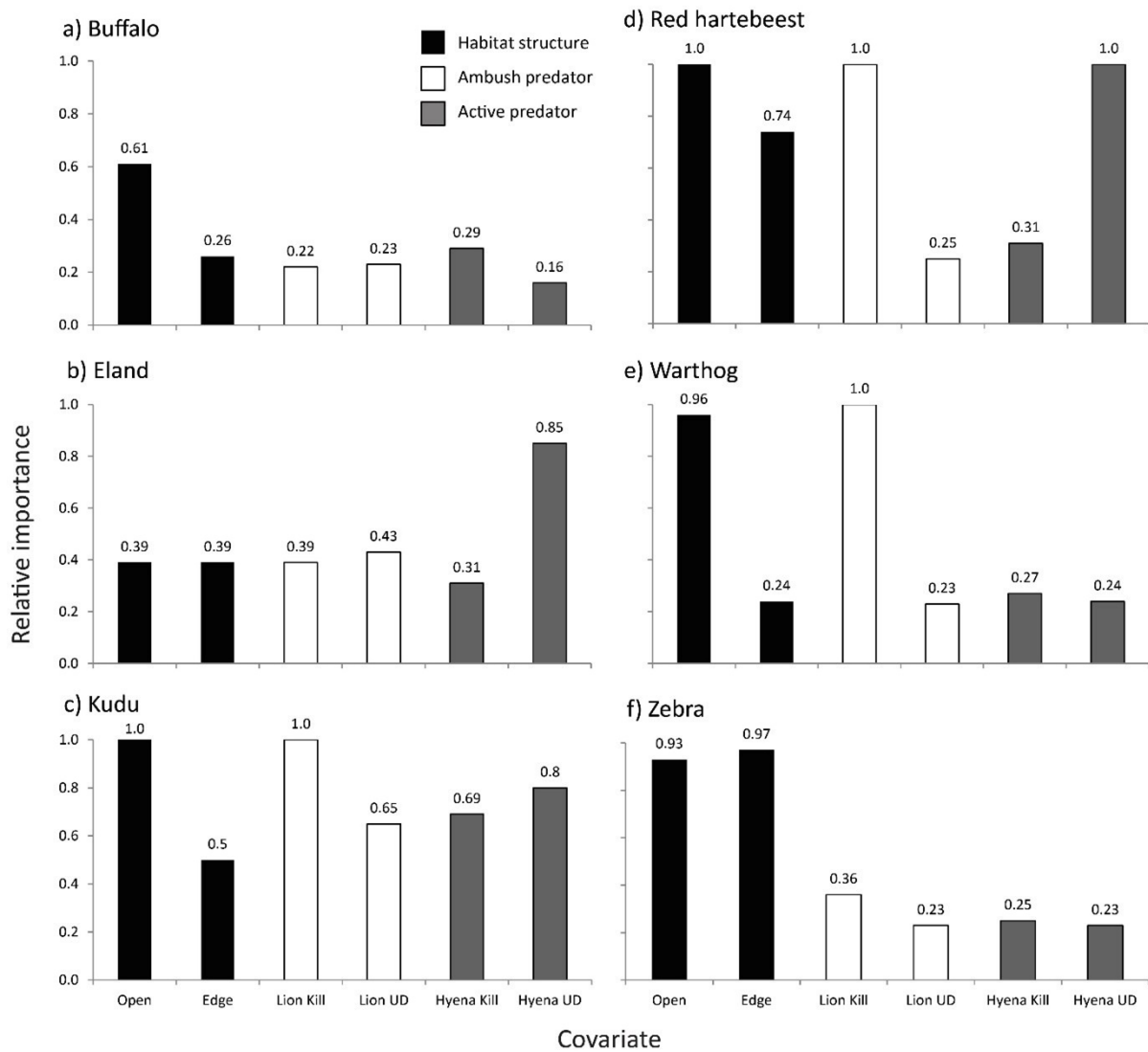
Figure 3. Statistically significant ($\alpha \leq 0.01$) spatially-explicit mixed effects regression trends derived from model-averaged coefficients from models describing ungulate aggregation in Addo Elephant National Park, South Africa (2003-2005). Shaded areas represent 95% confidence intervals.

647 Figure 1.



648

649 Figure 2.



650

651 Covariate definitions: Open = proportion open habitat, Edge = length of hard edge, LionKill =

652 odds ratio lion kill occurrence, LionUD = lion UD percentile, HyenaKill = odds ratio of hyena

653 kill occurrence, HyenaUD = hyena UD percentile.

654 Figure 3.

